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Phenological patterns of oribatid mites in an evergreen-sclerophyllous formation (Hortiatis, Greece)

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With 6 figures

Synopsis: *Original scientific paper*
The phenology of oribatid mites of a *Q. coccifera* forest (mediterranean-type ecosystem) was studied on Mt Hortitiatis (Greece). The population density of most species displayed seasonal patterns which parallel the seasonal fluctuations of the mediterranean climate. The life cycle of three species was intensively explored and their life history characteristics are discussed. Precosity and iteroparity are traits common to each species. Nevertheless, the phenology of these species shape three patterns differing with regard to the timing of juvenile life stages development. *S. cf. latipes* inhabiting sheltered habitats underneath *Q. coccifera* shrubs lay eggs in winter-spring and the immatures can develop during summer. The eggs of *A. oudemansi* laid in winter-spring in mossbanks bordering *Q. coccifera* shrubs overcome summer drought remaining in quiescence and the immatures develop during autumn. Although two main periods with gravid females were recorded in winter and summer for *P. allifera*, it laid eggs the year round in open sites. They withstand the summer stress and the immatures develop during autumn. The development of immature life stages over short periods when smooth fluctuations of the environmental variables occur, coupled with precosity and iteroparity, were considered the life history strategies of the mediterranean species at Mt Hortiatis.

Key words: Acari, Oribatids, Mediterranean type ecosystems, Phenology, Life history strategies.

1. Introduction

The function of mediterranean type ecosystems is controlled by the mediterranean type climate characterized by a mild and wet winter coupled with a hot and dry summer. Maquis occupies the wet end of mediterranean type ecosystems (Mooney et al., 1970). In a previous paper we described the spatial and temporal organization of the community of oribatid mites inhabiting the organic layers of an evergreen-sclerophyllous formation at Mt Hortiatis dominated by *Quercus coccifera* [Asikidis & Stamou, 1991]. In this paper we provide information on the phenological patterns of oribatids. Particularly we aim to investigate the extent to which population dynamics of oribatid species are affected by the mediterranean type climate.

2. Materials and methods

Information concerning site characteristics, sampling design and extraction methods are given elsewhere (Asikidis & Stamou, 1991). The phenology of oribatids was studied monthly from November 1985 to December 1986. All specimens of the species *Scheloribates cf. latipes*, *Galumna allifera* and *Achipteria oudemansi* were treated with 35% lactic acid for three days. They were then examined microscopically for the life stage of immatures, the sex of adults and the number of eggs in the hysterosoma of females.

Census data were analysed by the method proposed by Stamou & Sgardelis (1989). Firstly they were smoothed using the filter $y_t = \sum_1^3 x_i/3$. Then the deterministic component of the model suggested by Stamou (1986), $y_t' = \exp\{a + b\cos(2\pi y_t + \varphi)/T\}$ (where φ = phase determining the position of the population density peak, T = period, a and b are constants), was numerically fitted to smoothed data. The description of the timing of an oribatid's life cycle was based upon consideration of the parameters φ and T, while the ratio b/a was used as a measure of the duration of occurrence of a certain life stage in the field.

3. Results

3.1. General

The fluctuations of the mean monthly temperature at the litter/humus interface of *Q. coccifera* are depicted in fig. 1. The annual temperature range at Hortiatis (−1 to 36 °C), exceeds the one recorded in an oakwood of Mt Holomon, 70 km east of Hortiatis (Stamou, 1981), while it is comparable to the corresponding range recorded in a phryganic ecosystem, 500 km south of Hortiatis (Sgardelis, 1988).

Data concerning the water content of the organic layers of *Q. coccifera* shrubs are shown in fig. 2. Iatrou (1989) suggested a logarithmic equation relating air relative humidity inside the organic layers of *Q. coccifera* to their water content. Applying this equation to

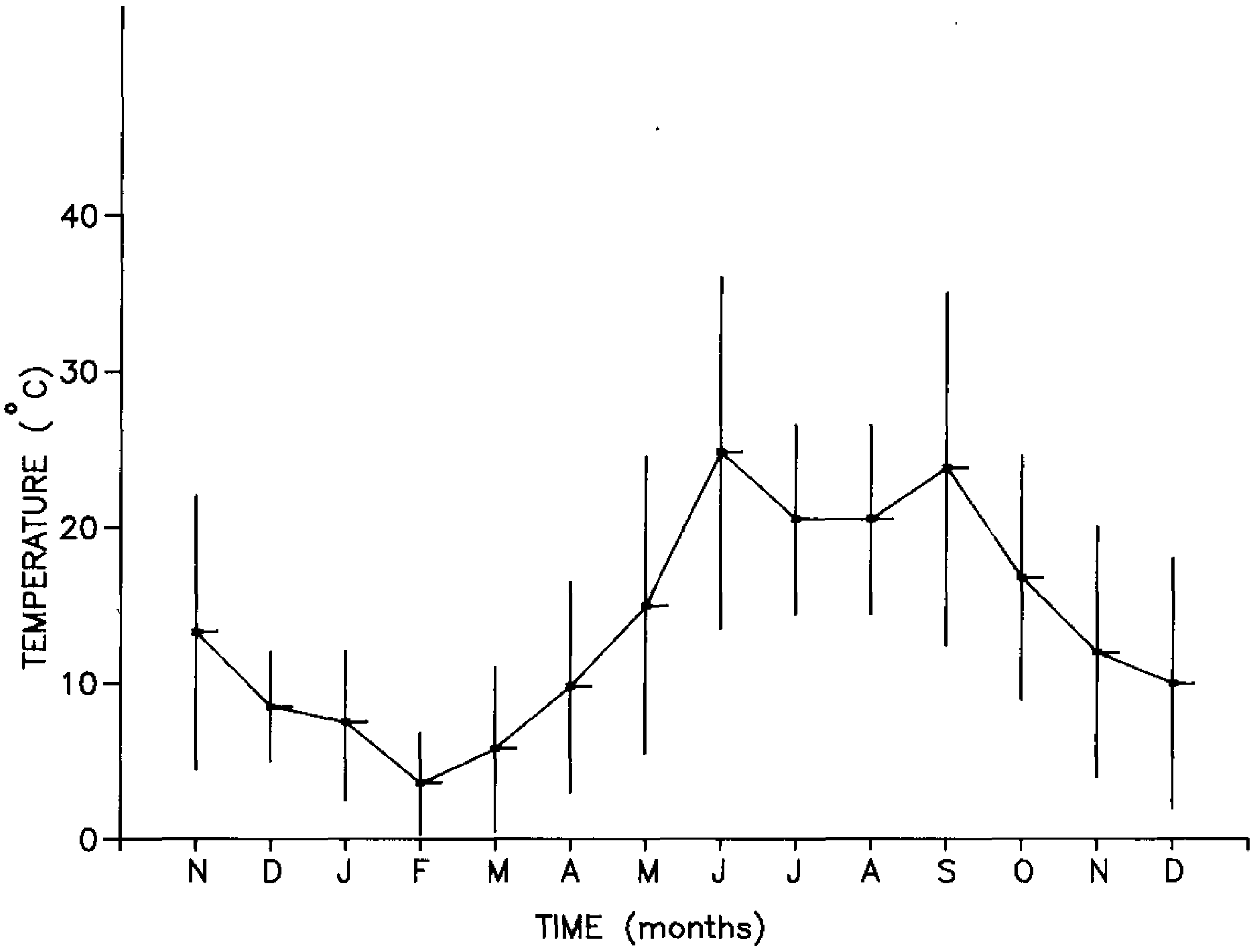

Figure 1. Maximum monthly, mean monthly and minimum monthly temperature recorded during the period from November 1985 to December 1986 at the interface litter/humus of *Q. coccifera* shrubs.

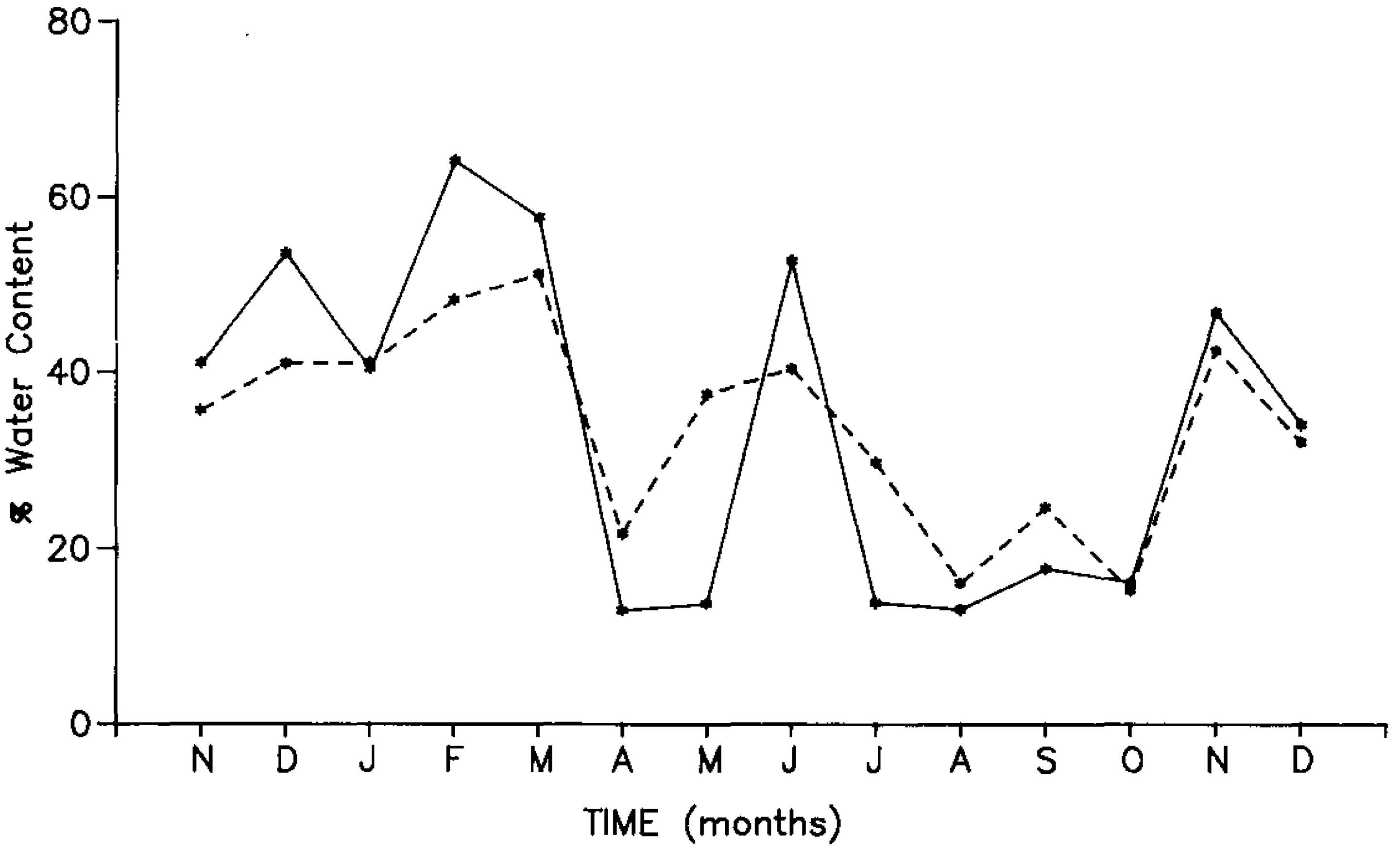

Figure 2. Mean monthly water content of litter (———) and humus (-----) of *Q. coccifera* recorded from November 1985 to December 1986.

Table 1. List of oribatid species sampled in six microsites at Mt Hortiatis.

	A	B	C	D
Sphaerochthonius splendidus (BERLESE)	10604	winter	winter-spring	humus
Camisia horrida (HERMANN)	76		winter & summer	lichens
Camisia spinifer (C. L. KOCH)	48		winter	lichens
Liodes ionicus (SELLNICK)	322	autumn-winter	the year round	lichens & grass
Licnodamaeus pulcherrimus (PAOLI)	2500	winter	winter	humus & litter
Damaeus sp.	19	autumn	summer-autumn	litter
Metabelba pulverulenta (C. L. KOCH)	69		winter & summer	moss & humus
Microppia minus (PAOLI)	1345	spring & autumn	winter & summer	humus
Medioppia obsoleta (PAOLI)	1819	summer-autumn	winter-spring	litter
Multioppia sp.	1055	autumn	autumn-winter	humus & moss
Quadroppia michaeli (MAHUNKA)	367	autumn	winter	humus & litter
Hermaniella granulata (NICOLET)	606	winter	winter	everywhere
Carabodes minusculus (BERLESE)	1485	autumn & spring	January & May	lichens & moss
Carabodes sp.	152	summer-autumn	winter	moss
Tectocepheus velatus (MICHAEL)	506	autumn	autumn-winter	moss
Xenillus tegeocranus (C. L. KOCH)	97		autumn-winter	moss
Oribatula sp.			December	everywhere
Protoribates capucinus (BERLESE)	281	autumn	winter	grass
Zygoribatula cognata (OUDEMANS)	591		November & December	*J. oxycedrus*
Scheloribates cf. latipes (C. L. KOCH)	814	summer	winter & summer	everywhere
Scheloribates pallidulus (C. L. KOCH)	68		autumn-winter	lichens & moss
Zetorchestes micronychus (BERLESE)	300	autumn	the year round	moss & litter
Pilogaluma allifera (OUDEMANS)	217	winter & summer	autumn-winter	litter, moss & *J. oxycedrus*
Achipteria oudemansi (VAN DER HAMMEN)	330	autumn	autumn-winter	moss & grass
Eupelops cf. holophilus (PEREZ-INIGO)	104	autumn	autumn-winter	lichens & grass
Peloptulus cf. phaeonutus (C. L. KOCH)	99	autumn	autumn-winter	grass
Rhysotritia ardua (C. L. KOCH)	251	summer	winter	*J. oxycedrus*
Steganacarus pulcherrimus (BERLESE)	76	autumn	winter-spring	litter

Note: Mean monthly population density (A), egg deposition period (B), period when population display higher density (C) and site where population has the mode of its spatial distribution are shown.

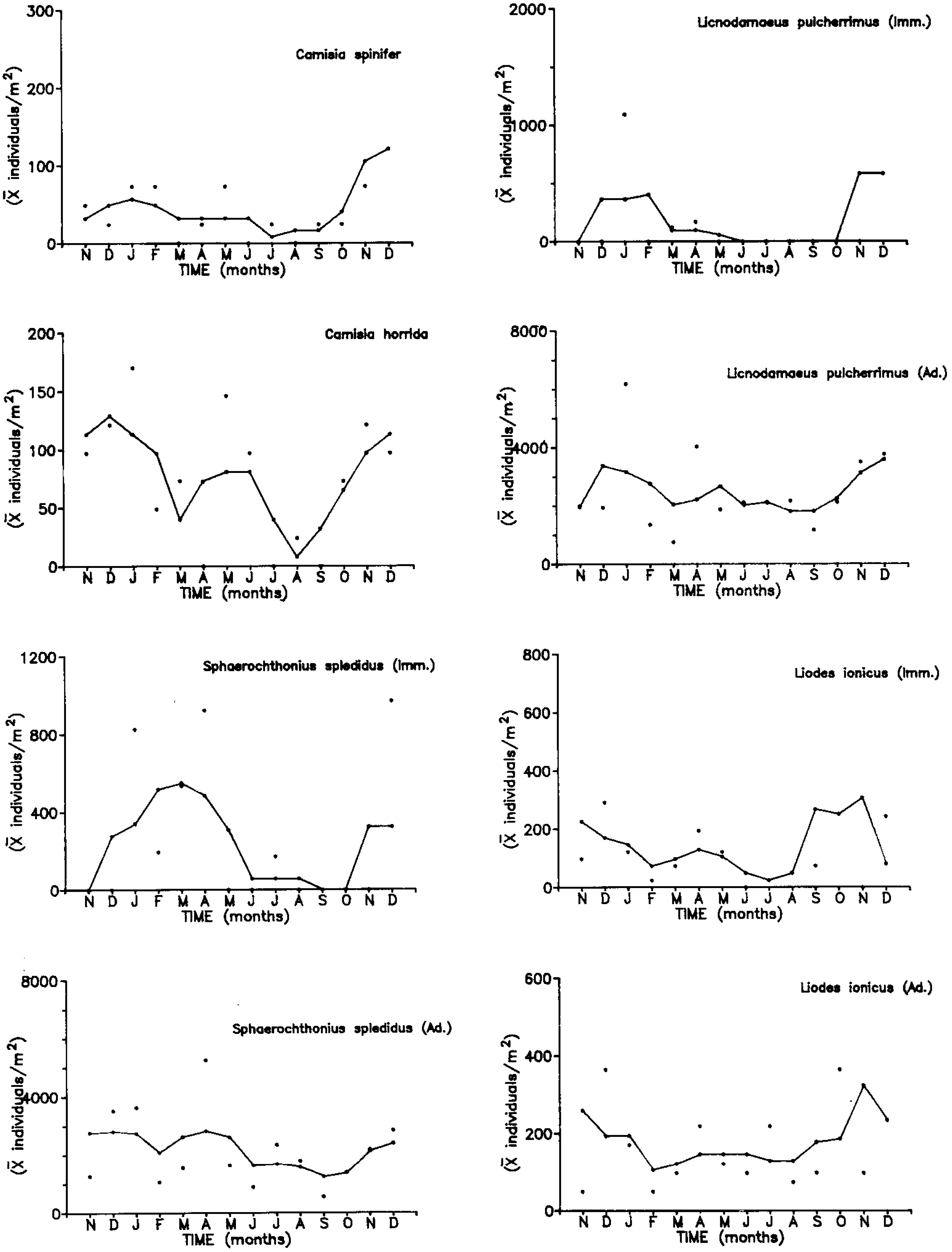
Camisia spinifer
(X̄ individuals/m²)
300
200
100
0
N D J F M A M J J A S O N D
TIME (months)
Licnodamaeus pulcherrimus (Imm.)
2000
1000
0
Camisia horrida
200
150
100
50
Licnodamaeus pulcherrimus (Ad.)
8000
4000
Sphaerochthonius spledidus (Imm.)
1200
800
400
Liodes ionicus (Imm.)
800
600
400
200
Sphaerochthonius spledidus (Ad.)
Liodes ionicus (Ad.)

Figure 3a

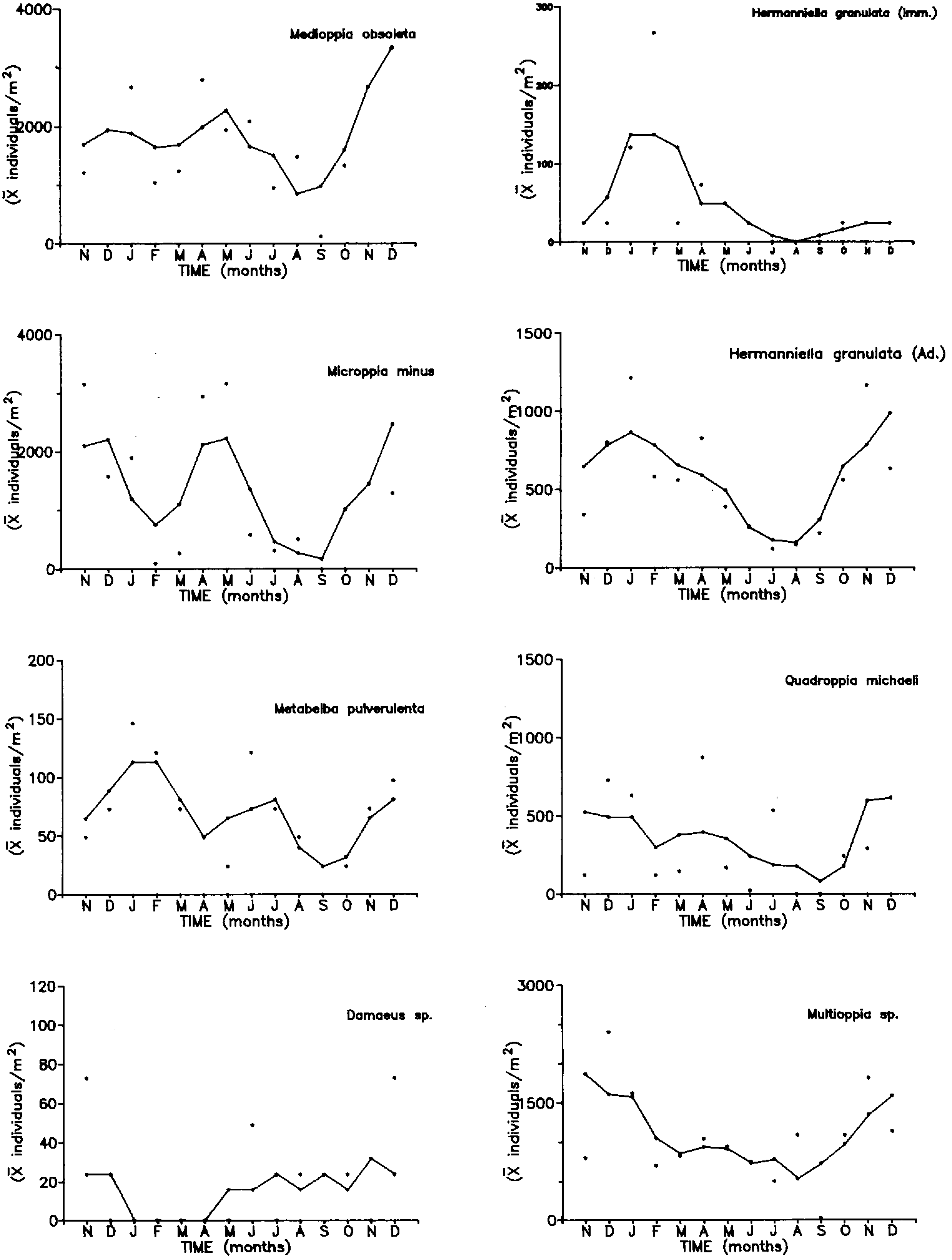
Mediloppia obsoleta
Hermanniella granulata (Imm.)
Microppia minus
Hermanniella granulata (Ad.)
Metabelba pulverulenta
Quadroppia michaeli
Damaeus sp.
Multioppia sp.
(X̄ individuals/m²)
4000
2000
0
300
200
100
1500
1000
500
150
50
120
80
60
40
20
3000
N D J F M A M J J A S O N D
TIME (months)

Figure 3b

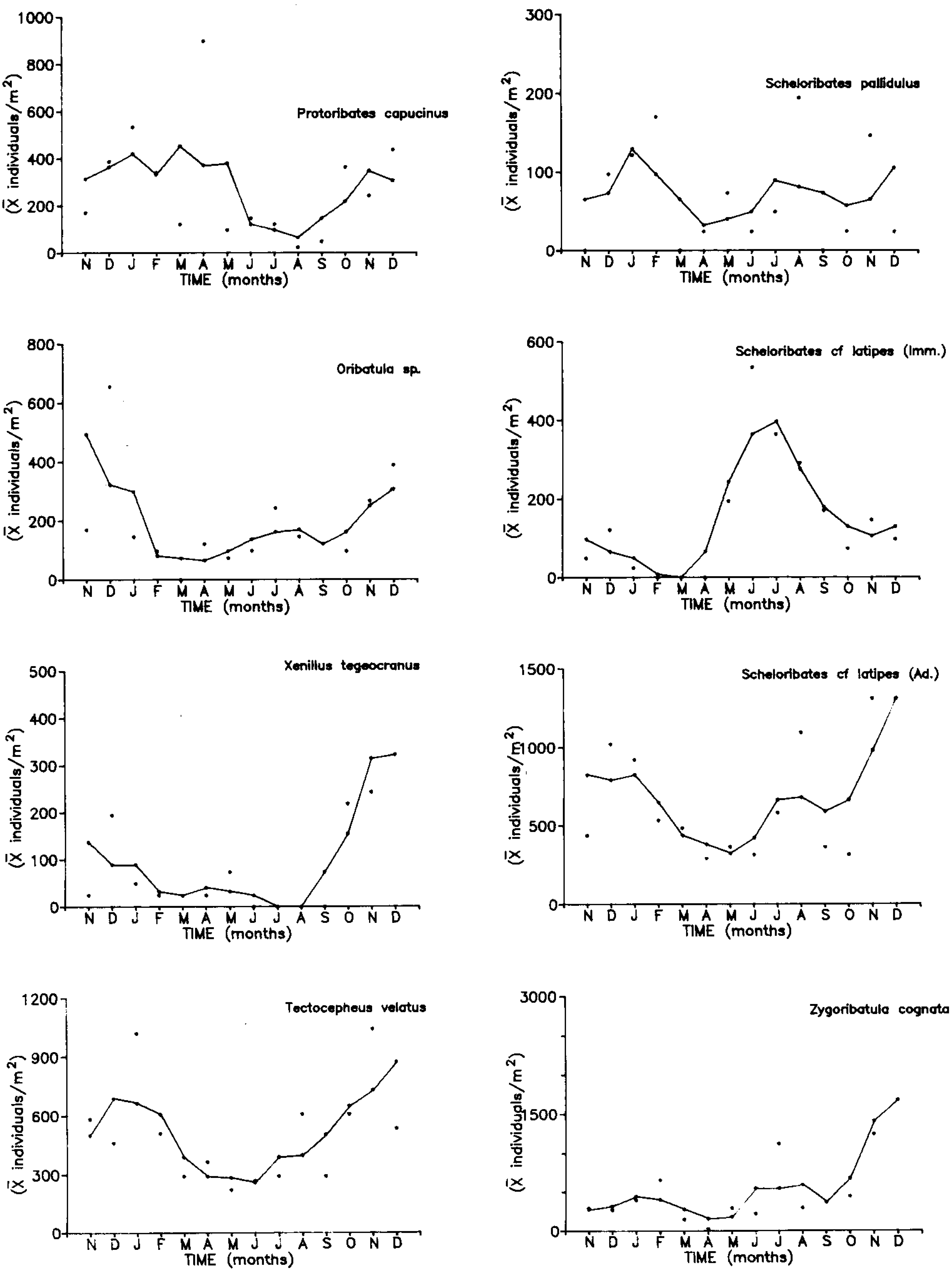
Protoribates capucinus
Scheloribates pallidulus
Oribatula sp.
Scheloribates cf latipes (Imm.)
Xenillus tegeocranus
Scheloribates cf latipes (Ad.)
Tectocepheus velatus
Zygoribatula cognata
(X̄ individuals/m²)
TIME (months)
N D J F M A M J J A S O N D
0
100
200
300
400
500
600
800
900
1000
1200
1500
3000

Figure 3c

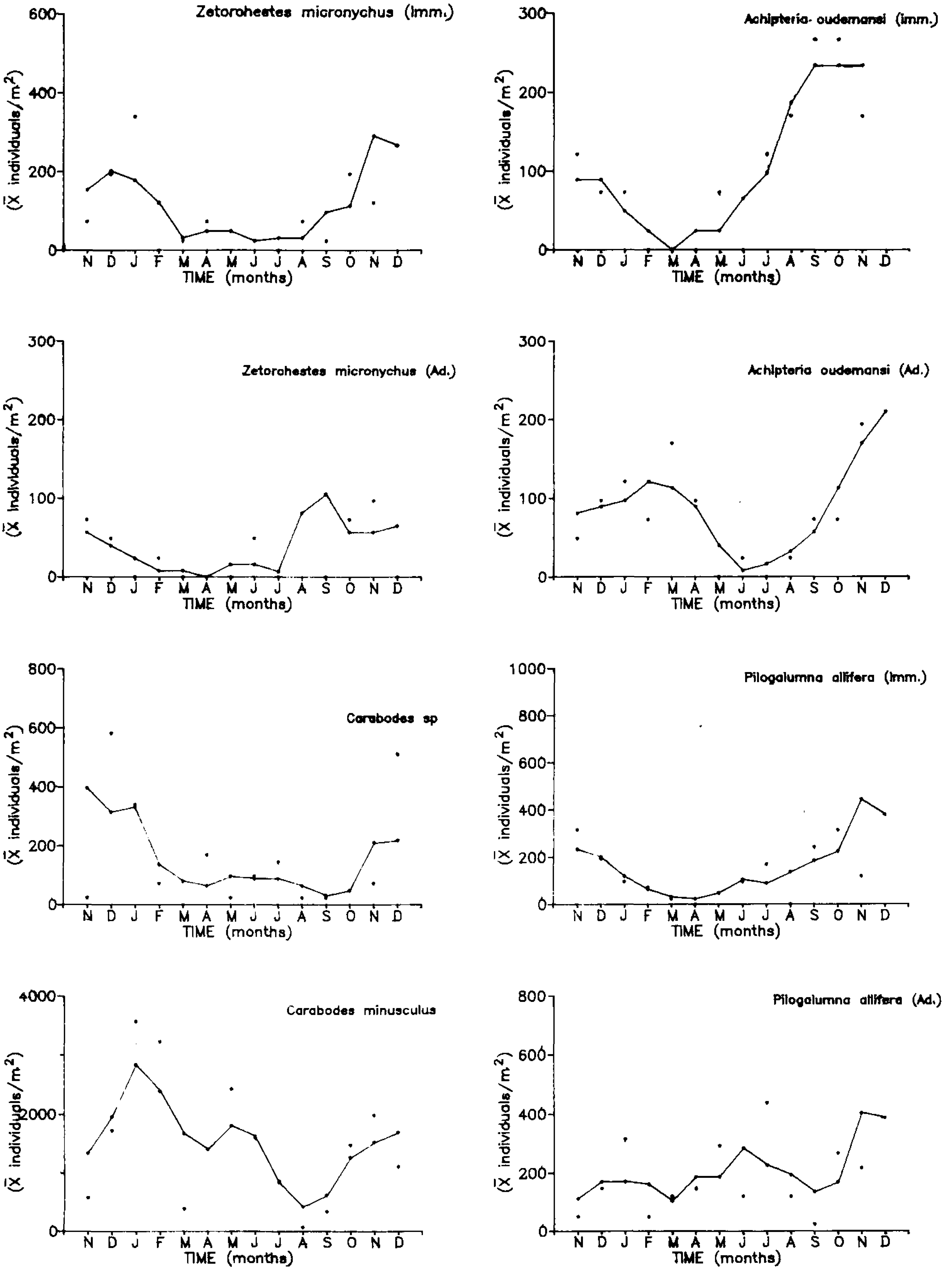
Zetorohestes micronychus (Imm.)
Achipteria oudemansi (Imm.)
Zetorchestes micronychus (Ad.)
Achipteria oudemansi (Ad.)
Carabodes sp
Pilogalumna allifera (Imm.)
Carabodes minusculus
Pilogalumna allifera (Ad.)
(X̄ individuals/m²)
TIME (months)
N D J F M A M J J A S O N D
0
100
200
300
400
600
800
1000
2000
4000

Figure 3d

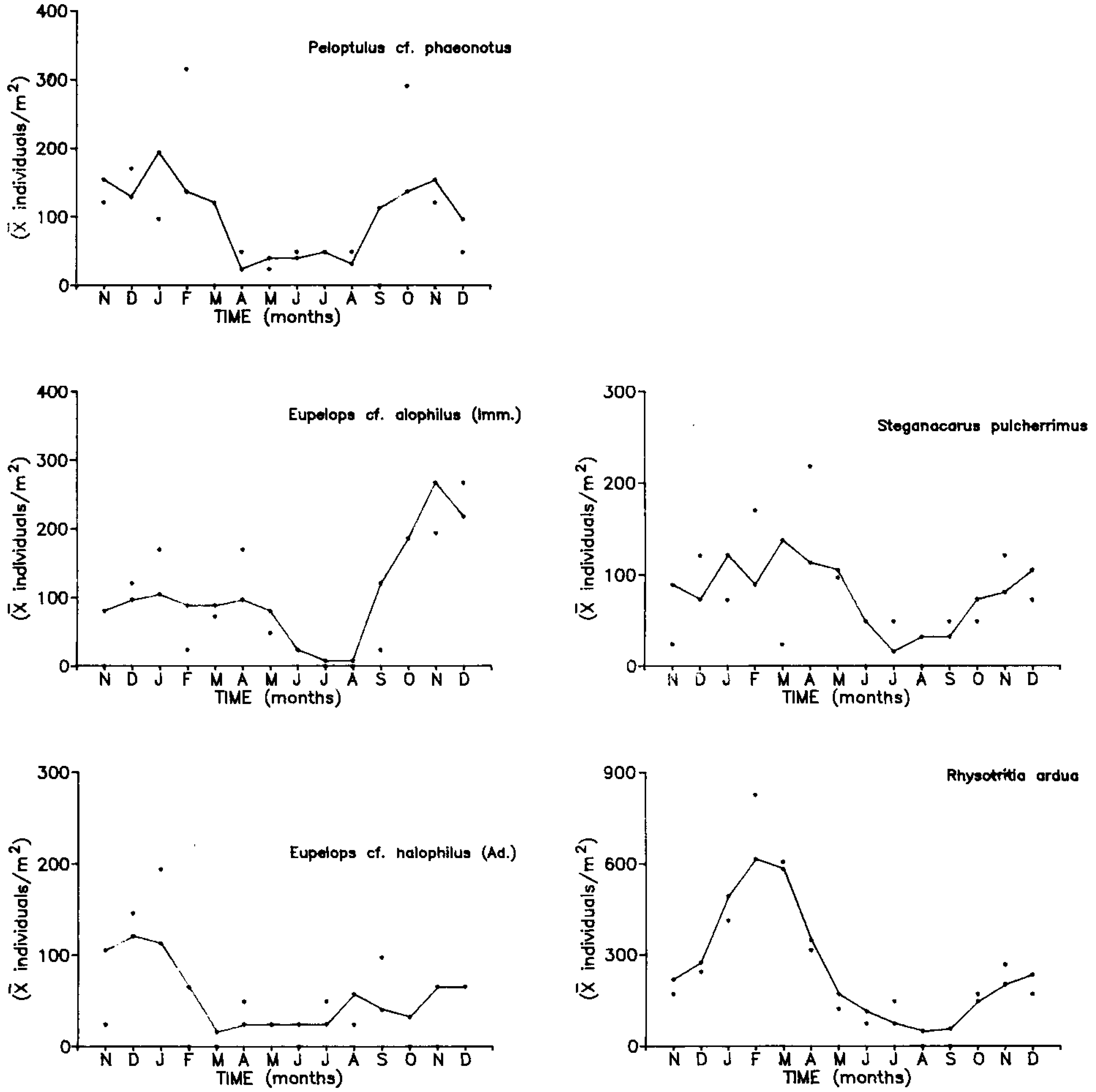

Figure 3. Monthly oscillations of population density m^{-2} of oribatid mite populations at Mt Hortiatis.

our data we estimated that the minimum RH% values in the litter and humus layers were 65 and 70% respectively. Finally, it should be noted that environmental hazards, that is wide diurnal fluctuations of temperature and humidity, were recorded mainly during late spring and early summer.

From the temporal and spatial distribution characteristics of the oribatid species sampled (tab. 1 & fig. 3) the following conclusions may be drawn: Most oribatids initiated a single generation a year and only *Camisia horrida*, *Microppia minus*, *Medioppia obsoleta*, *Metabelba pulverulenta* and *Carabodes minusculus*, initiated two generations per year. Most of the latter species displayed high adult population densities during the unfavourable time periods in winter and summer and had the mode of their spatial distribution in sheltered habitats. From the species initiating a single generation a year, nine displayed maximum population density in autumn-winter, eight in winter, two in winter-spring, one in summer-autumn and three had constant population density the year round. *S. cf. latipes* has the mode of its spatial distribution in the organic layers of *Q. coccifera*, *Achipteria oudemansi* is one of the numerically most important species characterizing the composition of the community in the open sites, and adults of *Pilogalumna allifera* are associated with open sites while its immatures are linked to the organic layers of *Juniperus oxycedrus* shrubs. The phenology of these species was intensively studied.

3.2. Phenological patterns

3.2.1. Scheloribates cf. latipes

The model fitted to smoothed census data (tab. 2 & fig. 4) shows a density peak for adults in November – December ($\varphi = 0.8$; the value $\varphi = 0$ was assigned to November). The low value of the ratio b/a (= 0.14) indicates that adults were numerous in the field for a long time period. The decline of adult numbers in winter 1986 (T = 15.7) appears to have been delayed probably due to the mild weather permitting the hatching of tritonymphs.

Gravid females were recorded almost the year round although higher values of the proportion of eggs per female were recorded during the period from February to July and the model produces a peak in late March ($\varphi = 5.9$). It seems likely that egg deposition and egg hatching occurred in spring.

The population density of larvae increased from April to peak in June – July ($\varphi = 8.6$) and about 2.5 weeks later the density peak for protonymphs occurred ($\varphi = 9.2$). Protonymphs were numerous in the field for a longer period than the larvae since the value of the ratio b/a for protonymphs was 0.93 instead of 1.11 as it was for larvae.

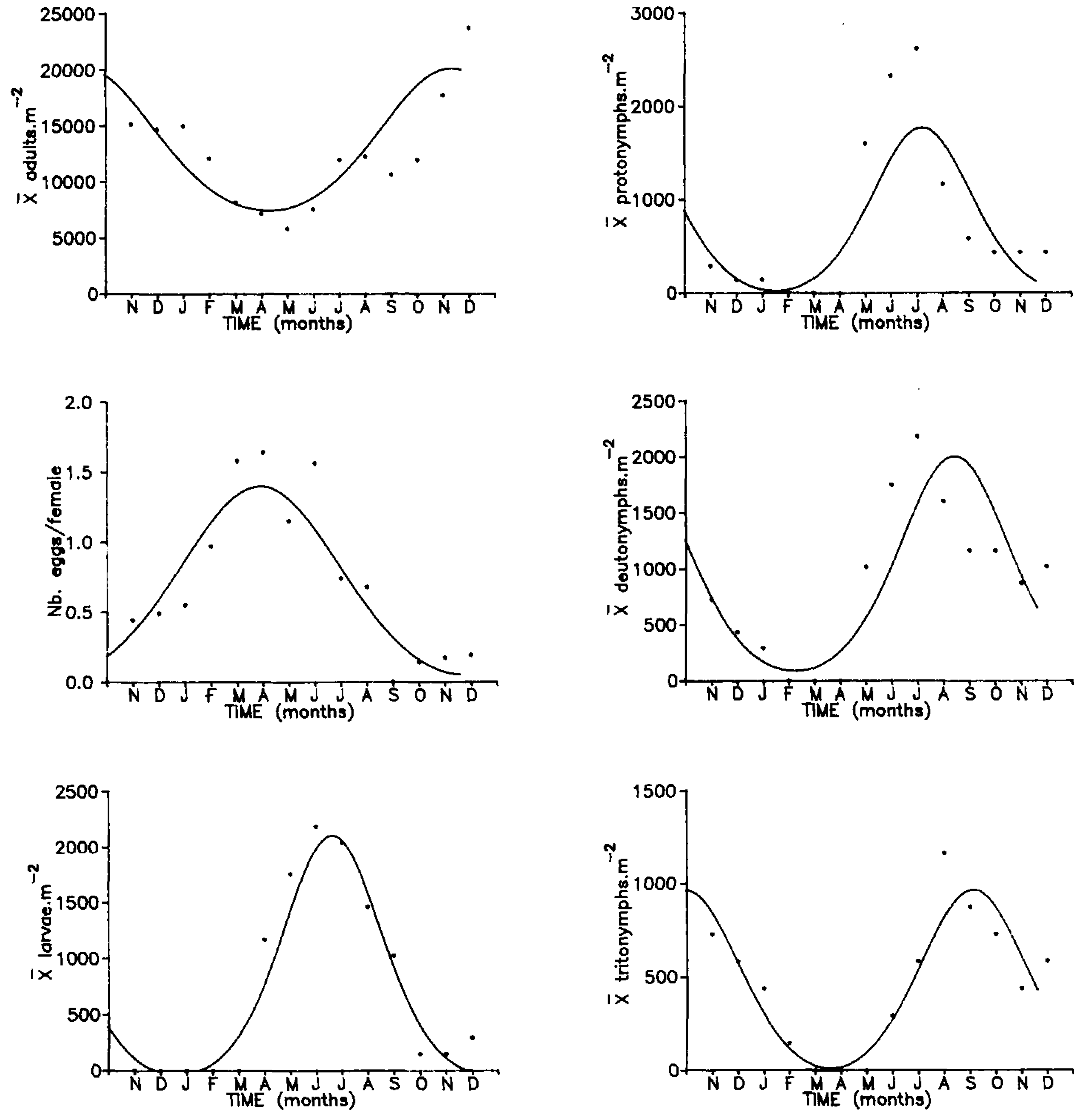

Figure 4. The fitting of the seasonal model on smoothed census data for the life stages of *Scheloribates cf. latipes*.

Table 2. The parameters of the phenological model fitted to smoothed census data of the life stages of three oribatid species.

Life stages	φ	T	b/a
Scheloribates cf. latipes			
Adult	0.8	15.7	0.14
Eggs/female	5.9	15.7	0.89
Larva	8.6	12.0	1.11
Protonymph	9.2	11.4	0.93
Deutonymph	10.4	12.4	0.81
Tritonymph	11.1	11.1	0.97
Pilogalumna allifera			
Adult	2.9	5.3	0.16
Eggs/female	4.0	5.1	0.25
Larva	11.1	12.6	1.04
Protonymph	13.4	14.4	0.34
Deutonymph	13.4	13.9	1.16
Tritonymph	14.2	15.1	1.30
Achipteria oudemansi			
Adult	3.8	10.3	0.5
Eggs/female	4.5	8.3	1.4
Larva	12.0	15.4	1.4
Protonymph	0.4	11.9	1.5
Deutonymph	0.8	12.7	1.0
Tritonymph	1.4	10.8	0.8

Note: For definition of parameters see text

The peak population density for deutonymphs occurred in August ($\varphi = 10.4$) and they were numerous in the field for a longer period than protonymphs ($b/a = 0.81$). The population density peak for tritonymphs occurred in September ($\varphi = 11.1$) and they developed into adults by the end of autumn.

The above data enable us to describe the timing of the life cycle of *S. cf. latipes* in the field. Adults become gravid soon after they attain adulthood. This species initiates a generation a year from eggs laid during spring. Eggs hatch three months later into larvae. Immature life stages develop rapidly during summer and tritonymphs are numerous in the field in early autumn. These latter develop into adults within three months, i.e. by the beginning of winter.

3.2.2. *Pilogalumna allifera*

High numbers of adults were recorded the year round ($b/a = 0.16$). Notwithstanding that the fitting of a seasonal model to such a data type was not statistically significant, it shows two density peaks in early January and June ($\varphi = 2.9, T = 5.3$) which is in accordance with smoothed data (fig. 5). The adults sampled in winter did not have a fully developed pigmentation and were probably recently emerged from tritonymphs. Following SGARDELIS *et al.* (1981), the density peak appearing in June may be attributed to animals emigrating to surface ground layers from the upper plant parts in order to deposit eggs. The females carried eggs throughout the year but the model produces two peaks in winter and summer ($\varphi = 4$, $T = 5.1$).

Larvae increased in numbers from May to peak in September ($\varphi = 11.1$). The population density peak for protonymphs occurred in November ($\varphi = 13.4$). The density peak for deutonymphs and tritonymphs was also recorded in the same period. It seems that during late autumn protonymphs, deutonymphs and tritonymphs develop rapidly into later life stages. Indeed, the earlier instars were numerous in the field for longer periods than the later ones. The estimated values for the ratio b/a were 0.34 for protonymphs, 1.16 for deutonymphs and 1.30 for tritonymphs.

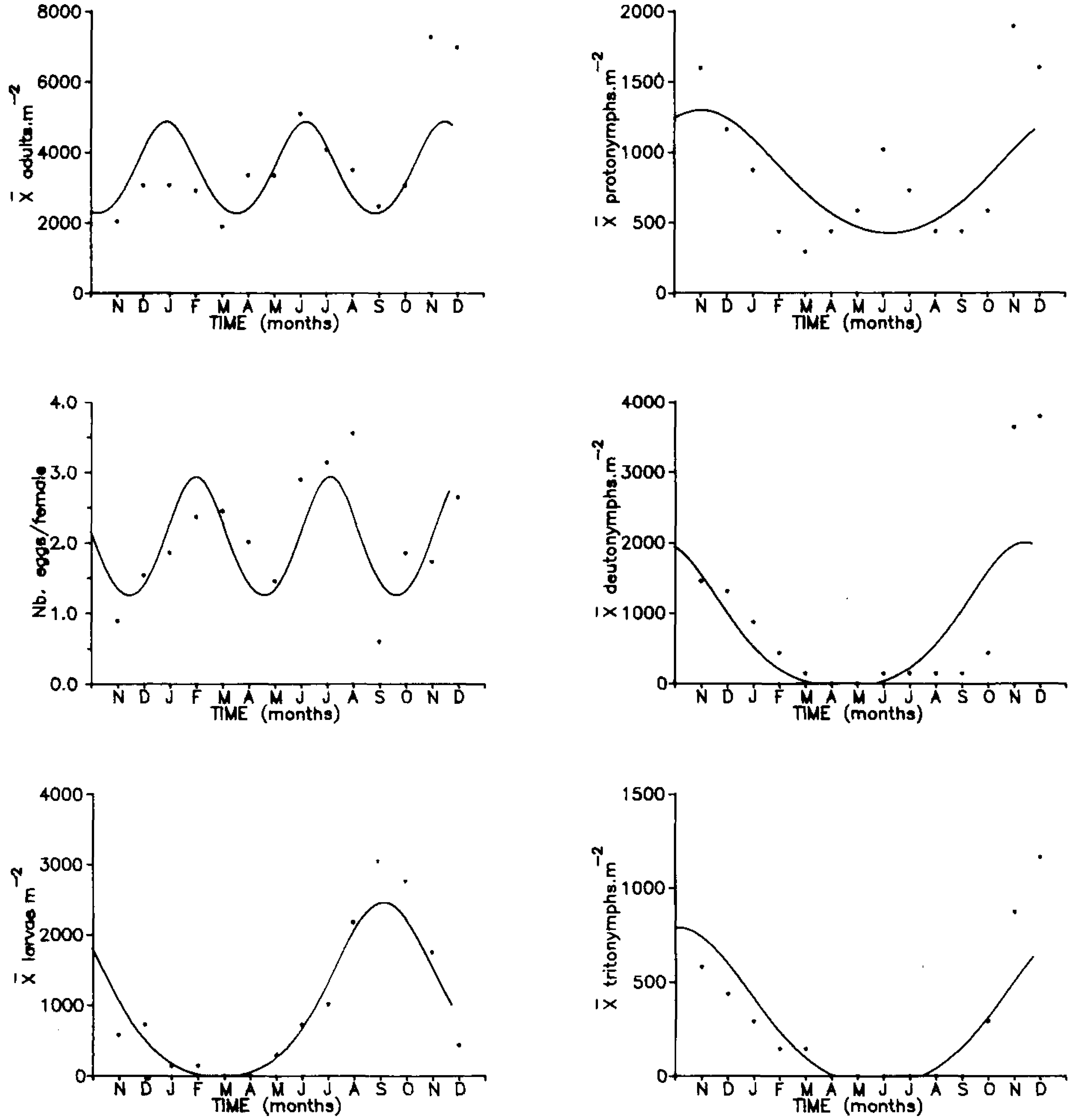

Figure 5. The fitting of the seasonal model on smoothed census data for the life stages of *Pilogalumna allifera*.

The above data allow the description of the life cycle development of *P. allifera* at Hortiatis. Adults become gravid soon after they emerge from tritonymphs and eggs are deposited in the field as soon as they are synthesized. Although females carry eggs the year round two main egg-deposition periods were recorded in late winter and in summer, the juvenile influx occurring in late summer. It seems likely that eggs laid during winter and spring withstand the late spring environmental hazards and the summer drought and hatch into larvae in autumn together with eggs deposited during summer. Next to the development of eggs, the development of juveniles seems also to slow down during late spring and summer. Thus, an overlap of immature life stages was recorded during autumn-early winter.

3.2.3. Achipteria oudemansi

The life stages of this species were present in the field for shorter periods than those of the preceding species. In fact, the values of the ratio b/a estimated for the life stages of *A. holomonensis* were greater than those determined for the corresponding life stages of the other species (the value determined for tritonymphs is excepted).

Adults were most numerous in winter and the model (fig. 6) yields a clear cut peak in late January ($\varphi = 3.8$). The model produces two peaks for the proportion of eggs per female in February—March (φ = 4.5), that is three weeks after the adult peak density and again in November (T = 8.3). This latter peak may be spurious in relation to the consistency of estimations, since in November few adults were sampled.

Larvae appeared in the field in early summer and were numerous in autumn, the density peak occurring in October 1986 (φ = 12). The protonymphs displayed a similar temporal pattern with a density peak in October—November (φ = 0.4) as did deutonymphs (φ = 0.8), while the population density peak for tritonymphs occurred one month later (φ = 1.4). (Notice that the peak density for tritonymphs in 1986 lies in October—November possibly due to the mild weather allowing the tritonymphal stage to moult rapidly). Thus, the development of larvae through protonymphs and deutonymphs into tritonymphs lasted for 1.4 months. The development of tritonymphs into adults lasted for 2.5 months. Tritonymphs were numerous in the field for the longest time (b/a = 0.8) and protonymphs for the shortest time (b/a = 1.5).

The timing of the life cycle of *A. oudemansi* is as follows: adults become gravid soon after they have attained the adult stage and eggs are synthesized and deposited from autumn to spring. The larvae are numerous in the field during the following autumn. The juvenile life stages develop rapidly into tritonymphs by the end of autumn and become adult by late winter.

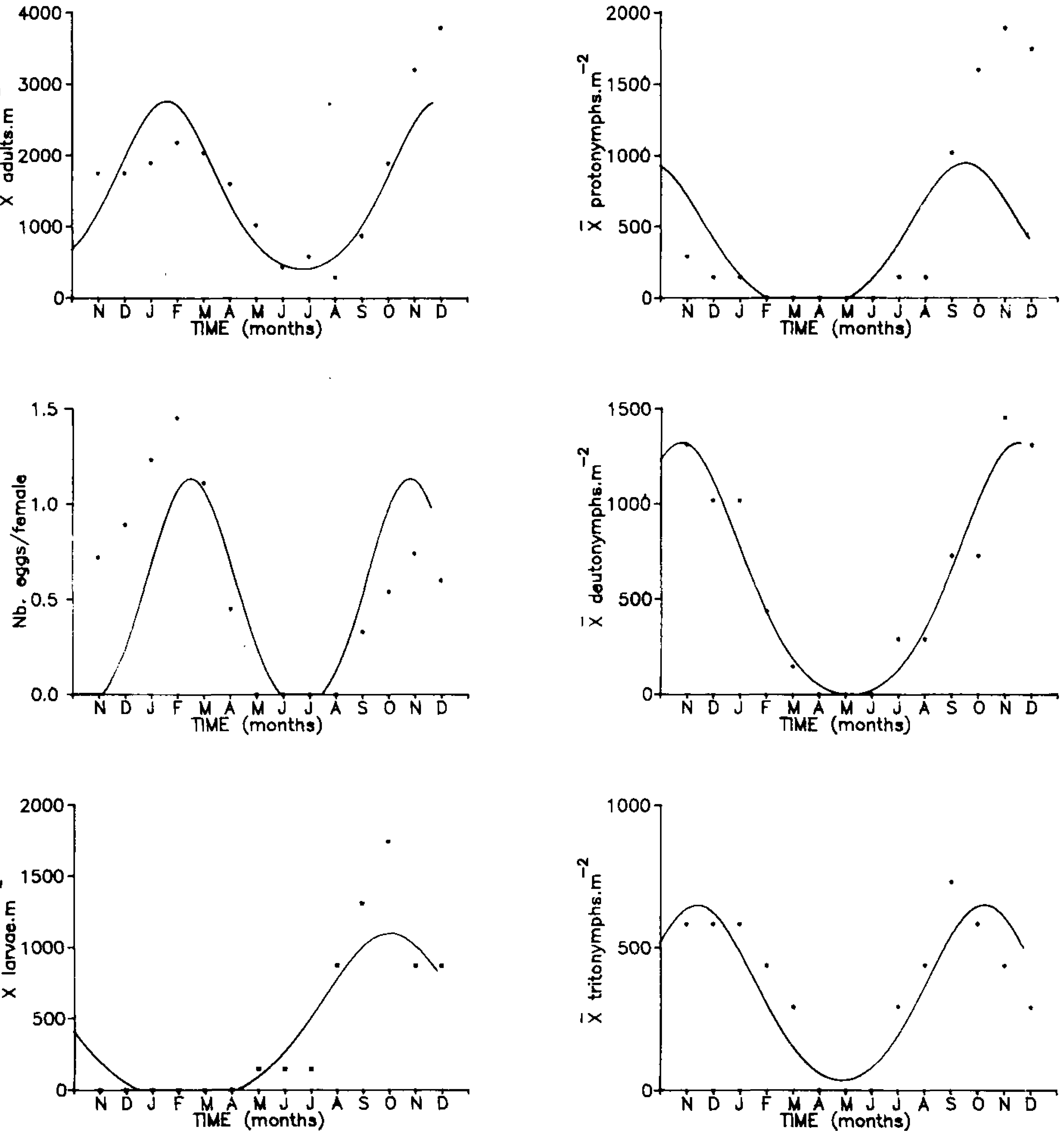

Figure 6. The fitting of the seasonal model on smoothed census data for the life stages of *Achipteria oudemansi*.

5. Discussion

As with populations occurring at Mt Holomon (STAMOU & SGARDELIS, 1989), most oribatids sample inside the *Q. coccifera* stand at Mt Hortiatis initiated a single generation a year.

The size of species initiating two generations a year is smaller than that of other taxonomically closely related species initiating a single generation a year. It is in agreement with suggestions made by LEBRUN (1971) that species with smaller size develop more rapidly than species with larger size. The adults of most species initiating two generations a year were abundant during the unfavourable time periods in winter and summer. With the exception of *C. minusculus* and *C. horrida* these species have the mode of their spatial distribution in protected microsites underneath shrubs. Also immatures of *C. minusculus* develop in sheltered sites inside specimens of the lichen *Cladonia foliacea* (unpubl.).

The life cycles of the three species intensively assessed display large areas of similarity. Adults are numerous in the field during winter and, as for other oribatid species it represents the overwintering life stage (LUXTON, 1981a, STAMOU & SGARDELIS, 1989). Eggs are synthesized and deposited soon after the adult reach adulthood in late winter-early spring. Similar results are also reported for other oribatid species e.g. *Tectocepheus velatus* from a Danish woodland (LUXTON 1981b), *S. latipes*, *Achipteria holomonensis* and *Damaeus balcanicus* from a Greek woodland (STAMOU & SGARDELIS, 1989). Females carry eggs almost the year round and all the three species appear iteroparous. According to BEGON *et al.* (1986), precosity and iteroparity characterize organisms capable of combatting adversity. In all three species the development of juvenile life stages take place over short time periods. Finally, their life cycle development displays annual periodicity. In spite of the above similarities, the life cycle development of these species illustrates three distinct temporal patterns differing with respect to the timing of eggs hatching and juvenile development. As a matter of fact, the eggs of *S. cf. latipes* hatch in late spring and the juvenile life stages develop rapidly during summer. Eggs of *A. oudemansi* and *P. allifera* overcome summer drought remaining dormant (ASIKIDIS, 1989) and hatch during autumn when immatures develop rapidly into adults. *P. allifera* in particular, deposit eggs mainly in open microsites between *Q. coccifera* shrubs, has two main egg-laying periods.

Oribatids at Hortiatis have to encounter environmental severity in summer, while wide diurnal fluctuations of temperature and humidity occur mainly during late spring and early summer. Their life cycle development displays seasonality which parallels the seasonal oscillations of the mediterranean climate. Thus, it can be said that the development of their life cycle is controlled rather by external factors, i.e. the regular fluctuations of environmental variables and the environmental hazards, than by intrinsic population factors like inter- and intra-specific relationships. An analogous suggestion has also been reported by STAMOU & SGARDELIS (1989) for three oribatids from Mt Holomon and by BLOCK (1985) for arthropods inhabiting antarctic habitats. It is thought that, in general, the life cycle development of oribatids is controlled by external factors like the onset of litterfall, precipitation, temperature and so on (e.g. USHER 1975; THOMAS, 1979; LUXTON 1981b; & COURBIER *et al.*, 1985). LUXTON (1981 a & b) suggested that in temperate regions the external signals act to trigger the onset of the life cycle development of oribatids. Our point for oribatids inhabiting mediterreanean regions differ from the above suggestion in that the external signals are not considered as environmental indicators. In mediterranean regions the effect of seasonal and predictable year to year fluctuations of environmental variables on the life cycle development exceeds that of environmental hazards (SGARDELIS, 1988; ASIKIDIS & STAMOU, 1991) and the timing of an oribatid's life cycle is organized to synchronize with regular environmental oscillations. Analogous conclusions has been arrived at also by STAMOU & SGARDELIS (1989) studying the temporal patterns of oribatids from a region with climate transient between mediterranean and temperate. Triggered life cycle development involves some kind of long-term physiological compensation which might be lacking from mediterranean species. So, the development of immature life stages is confined to short time periods when smooth fluctuations of environmental variables occur.

The development of an oribatid's life stages confined to short periods may be considered as an adaptation to a regular, although widely oscillating environment, while precosity coupled with iteroparity should be considered as an adaptation against environmental hazards. In any case, although in all three species the adult is the overwintering life stage, the life cycle timing of each one responds in a different way to the seasonal environment. *S. cf. latipes* living in sheltered sites underneath *Q. coccifera* shrubs is able to develop during summer. *A. oudemansi* lays eggs over a rather short period in partly sheltered habitats in the border of *Q. coccifera* shrubs and overcome summer drought by remaining in quiescence. *G. allifera* lays eggs in open sites throughout the year and eggs and larvae withstand summer drought and develop in autumn. Thus, the seasonal population dynamics pattern of each species seems to an extent to be typical of the species. So, it may be said that the community is structured of superimposed independent life cycles.

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